

THE WING-VENATION OF THE COLEOPTERA.*

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In the course of the last two generations, since the first attempts by Adolph (Nova Acta der Leop.-Carol. deutschen Akad. d. Naturf. 41(2), 213, 1880.) and Redtenbacher (Ann. d. k. k. naturhist. Hofmuseums I, 153, 1886) the comparative study of the wing-veins of the various groups of insects, supplemented by that of their larval tracheæ, has shown that all insect wings have a venation based on a common plan, whose modifications in the various orders are for the most part, well understood. In the Coleoptera, alone, of the larger orders, there is nothing approaching agreement in interpretation, for several reasons. In the first place the venation is sufficiently unique, and complicated, to make such a superficial study as brought even Adolph and Redtenbacher close to the truth in the Lepidoptera, for instance, almost completely futile. The complicated foldings also interrupt the veins and cause distortions in their courses. Further, the first forms studied for their pupal tracheation were specialized Cerambycidae, a family in which the tracheation is degenerate and no longer fully corresponds to the veins. Several workers, notably Kempers (Tijd. voor Entom. 42 to 45) and Kolbe (Archiv für Naturges. 67: Beiheft 89, 1901) have been thrown off by Adolph's or Woodworth's theories of an alternate system of convex and concave veins, which in the manner applied by them, is deceptive in the higher orders. More recently d'Orchymont has proposed a more carefully studied scheme, but his also ignores the evidence of the tracheation, and to me seems only half correct. Kühne's study of the tracheation (Zeits. wiss. Zool. 112: 692) alone has resulted in essentially the same conclusions which are expanded below. His paper is somewhat diagrammatically illustrated and appears to have been largely ignored by other workers; but I have verified his main conclusions, the differences between our results being mainly a matter of interpretation.

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In the present paper I shall try to identify the main veins of the Coleopterous wing with those recognized in other orders, and will suggest a tentative scheme of their branching. The main identifications, though differing from the several schemes which now hold the field, are supported by a convergence of evidence from the tracheation and basal sclerites, as well as by the character of the veins themselves.

In interpreting the tracheation my first assumption has been that each trachea which is separate in the most generalized form available, represents a single main vein, and that together all the veins are accounted for. In a single particular this assumption has been slightly modified—the identification of the first anal stem, as discussed below.

To take up the main veins in order:

Costa.—In all the orders of insects the costal vein lies along the costal edge of the wing, or is preceded only by a membranous strip, and runs far basad, forming a hook-like articulation with the body. It contains a weak trachea or none. In the Coleoptera studied the base of the costal edge is occupied by a vein, which in Calosoma contains a weak trachea. This is certainly *costa*. In a few forms (Silpha, Fig. 24, and Buprestidæ, for instance) there is a little membrane in front of it, but never another vein.

Subcosta.—In all the known orders of insects subcosta is immediately recognizable as a concave vein, that is, it lies at the foot of a trough in the surface of the wing, and its cavity is mainly below the level of the wing-membrane. The second vein from the costal edge in all the Coleoptera is so formed, and may be safely labelled *subcosta*. It contains a strong trachea in all the forms studied (the one labeled "C" by Comstock and Needham, who overlooked *costa*).

Radius.—The third vein of the wing is strongly convex, and forms the principal articulation with the thorax, together, that is, with the second axillary sclerite, from which it rises. Its trachea is always strong, and rises from the anterior tracheal trunk (Chapman, in Comstock's "Wings of Insects") running in front of the wing-process in close proximity to C and Sc. In the Coleoptera the third of the three closely crowded veins at the costal margin of the wing articulates in the proper manner, and contains the most posterior of the tracheæ arising from the anterior trunk, in every form studied, from Cicindela to the Cerambycidæ. It then is *radius*.

Media.—With media a more serious problem arises. Media is highly unstable in the various orders of insects and may associate itself as a branch with either radius or cubitus. In the Coleoptera whose tracheation is most complete, however, (Calosoma, Fig. 2, Dytiscus, Fig. 5, for instance, and some specimens of Tenebrio, Fig. 6), there is an independent trachea that can only be media. In Calosoma

and Tenebrio, at least, it arises from the posterior tracheal trunk, as in the majority of specialized insects. The corresponding vein is always weak, fading out at the base, and the trachea shows a strong tendency to weaken, and to lose its terminal portion to the neighboring tracheæ. In Tenebrio it is individually unstable, in some specimens independent, in others arising from the base of Cu. In many forms its basal part is a mere rudiment (labeled R in Comstock's "Wings of Insects," Figs. 309, 310), while its outer part has switched its connection to branches running up from Cu, or more rarely down from R. The weakness of this vein and trachea would characterize it as M, even were there not the further evidence of its position immediately following the unmistakable Sc and R. It is a "concave" vein, like M in the Lepidoptera and Neuroptera, and as in them it has no direct connection to the basal sclerites.

In all those Coleoptera whose basal venation is sufficiently spaced out, there is an arculus-like bar running across from the base of radius to Cu. This evidently represents an *anterior* arculus, being a short sector of vein M (Fig. 6), whose extreme base has fused with R, while it anastomoses immediately after, with Cu. In a few cases, where the medial trachea is independent, it can be plainly seen, passing from the radial to the medial vein-cavity through this bar.

Cubitus.—Cubitus is a strong convex vein. Here is perhaps the best opportunity for disagreement in interpretation. My identification is based, *first*, on the position and independence of the trachea in the Adephaga, which have the fullest tracheation, and in some specimens at least, of various Serricornis; *second*, on its basal connection with the axillary sclerite (though d'Orchymont considers this connection secondary, a result of fusion with the vein I interpret as 1st A); *third*, on the fact that the next vein (1st A) arises out of it near its base, just as the vein so called does in the Lepidoptera, and several other orders, and as the homologous vein (commonly called Cu₂) does in the Neuroptera and Trichoptera.

First anal.—The difficulty as to this vein is rather one of nomenclature than of homology, save only in the Phytophaga and Lamellicornis. In the most primitive orders there is an independent vein lying between Cu and the anal fan (1st A of Comstock's figures 116 to 124). This is in early forms fluctuating in position, and possibly even duplicated in a few cases (Comstock, Fig. 117, hind wing); attaching itself either to Cu or to the anal fan; but in almost all cases lies close beside the anal furrow. In the holometabolous orders it has become definitely associated with the cubital stem and appears like a branch of cubitus near the base. For this reason it is commonly treated as a branch of Cu in certain orders (e. g., the Neuroptera) and has been illogically labeled Cu₂. Of course if counted at all with the cubitals it would be Cu₃, as it would be the third branch of that stem. In other orders (as the Lepidoptera and Diptera) the connection with Cu is inconspicuous, either on account of a secondary splitting back, or through atrophy of the vein itself (butterflies); and the vein has been counted as independent, the true vein Cu₂ being correctly so labeled.

In the Coleoptera, save in the Phytophaga and some Lamellicorns, there is a trachea which splits off from Cu near its base, then frequently runs obliquely through the membrane, and enters a vein in the outer part of the wing, running with it to the margin (Figs. 3, 5, 6). The concave anal furrow lies close below this trachea. In Cupes (Figs. 4, 12) the whole is represented by a vein, and meets all the qualifications of 1st A (that is, Cu₃). In higher phytophaga at least, this trachea is completely absent, as shown by a Comparison of Comstock's figures 308 to 310, with mine of Tenebrio (Figs. 6, 43); and the corresponding vein of the imago is also absent.

Second and following anals.—There remain two branched tracheæ, and a third which is also bifurcated in the Adephaga, but more commonly simple. These may be numbered in order: 2d A, 3d A and 4th A. They doubtless represent the anal fan of lower orders, and also the second and third anals, and supporting vein of the jugum in, the Lepidoptera. The first of these is 3-branched at least, as shown plainly in the Buprestidæ (Figs. 6a, 34); but the anterior branch, both trachea and vein, is lost in many families, including all the Adephaga, Palpicornia and Heteromera; and the posterior branch, save in the Elaters, Lampyrids, and some Buprestidæ and Dermestidæ, fuses at the apex with the anterior branch of 3d A.

In this discussion the anals are treated as four in number on account of the tracheal arrangement, and seem to be homologous with the three recognized anals and the jugal brace of the Lepidoptera; but the condition in the base of the wing is complex, and comparison with *Chauliodes* (Fig. 71: a form which shows the same number of terminal anal branches) suggests strongly that the second may be a fusion of an original second and third anal; and that the vein here considered a cross-vein between 2d A and 3d A may really be a fourth branch of 2d A; in several forms it has a trachea.

The permanent cross-veins.—Certain cross-veins are so constant in higher insects as to become a part of the hypothetical plan. These are the *humeral*, the *arculus*, and a series near the middle of the wing (known as discocellulars in the Lepidoptera). The humeral cross vein shows plainly in several Coleoptera as a short fusion of C and Sc, which are everywhere closely parallel. Arculus is plain enough, especially in the Serricornes and Heteromera, (Figs. 65 and 66 for instance), and has already been discussed as a sector of media. The discocellulars, if present as such at all, are disguised by the folding, and must be discussed among the more problematical veins.

Stigma.—The stigma or pterostigma is a thickening of the marginal portion of the wing in the neighborhood of the apical part of Sc (Sc₂) and R₁. It shows plainly in a great many beetles belonging to the Adephaga, Palpicornia and Staphylinioidea, and will be used below as a means of identifying the distal sector of R₁.

THE FORKING OF THE VEINS.

Subcosta is so completely fused with costa and radius that a discussion of its outer course can lead to no certain conclusion. I have postulated a forking beyond the hinge, to account for one of the obscure cells at this point in the Carabidæ and the double thickening of the stigma in Hydrous. The fading out of the trachea of R_1 in those forms that have one at all, shows that the terminal portion of R_1 has been captured by Sc_2 (a common occurrence). In the more specialized forms Sc_2 is one of the tracheæ that persists, and with the disappearance of true veins in the apical part of the wing, takes an oblique course toward the apex regardless of what traces of veins remain (Fig. 5, 6a; but compare Fig. 6). The tracheæ of M and 2d A in certain forms behave similarly.

Radius.— R_1 is a vein that tends strongly to weaken and disappear, its terminal portion fusing with Sc. In several Coleoptera there is a plain anterior branch of the radial stem which continues in the common cavity of Sc and R beyond the point at which the main radial trachea leaves it (Fig. 2). There is no reason to doubt that this is R_1 , and that the main trachea, beyond the bifurcation, is the stem of R_s .

Beyond this point tracheation fails to give evidence, as the subdivisions of R_s are unstable in all the forms yet studied. The interpretation laid out on the hypothetical plan (Fig. 1) is based on the assumptions, *first*, that the apex of the wing in a low holometabolous insect is to be sought in the neighborhood of R_3 , and *second*, on the plain connection of the stub here identified as R_{4+s} across to the stem of R_s in such forms as Tetracha (Fig. 13). The terminal veining here introduced into the hypothetical plan is nowhere so plain as in Hydrous, but well-marked traces survive, not only in the other large Hydrophilidæ, but in the Lamellicorns as well. This group of veins might likewise be interpreted as M_{1+2} , but the strong tendency to reduction in the median and cubital systems of the Neuroptera would suggest a similar interpretation here.

In the Polyphaga the base of R_s is atrophied, leaving the outer part as an apparent backward-projecting spur—the *radial recurrent* (Rr). The second radial cross-vein, on the atrophy of a segment of R_s crossing the main folds, swings into this portion of R_s , and is usually reckoned with it as a portion of the radial recurrent, which would then be designated according to the usual terminology as R_s & 2d r.

Media.—Media has become two-branched in practically all the known Neuroptera, and in many is reduced to a single stem, forking only at a point corresponding to the nearly veinless apical region of the Coleoptera. The presence of but a single medial trachea in all the forms studied, save for unstable terminal branching, would suggest here that no branches need be sought save in the terminal portion of the wing. I have marked as medials those terminal veins that seem to connect most closely with the medial stem. The main trachea in the Aephaga, runs out in the vein here marked M_4 (Fig. 3); in the Polyphaga swinging into the same vein with Cu toward the margin. The two veins that survive in the generality of forms are marked M_1 and

M_4 because they are the extreme members of the complex group shown by Hydrous. They might be considered M_{1+2} and M_{3+4} if the extra veins of Hydrous be considered secondary.

In almost all forms (except a few Adephaga and Cupes) the base of media fades out, leaving the main part of it attached at the apex only. This sector of the vein is known as the *medial recurrent* (Mr).

Cubitus.—There is never but one vein supplied by the cubital trachea (leaving out of account the vein here treated as 1st A). Many Neuroptera also have only a single corresponding cubital, or a single main vein supplemented by some secondaries. To judge by the arrangement of these terminal branches the missing cubital branch has either fused completely with the surviving one, or has atrophied on the posterior side of it. At this point some Lamellicornes have a trachea not represented by any very distinct vein in the imago, which may possibly be the missing Cu_2 , but is more likely a last trace of 1st A.

In the Hydrophilidæ and Haliplidæ (Figs. 19 to 23), Cu runs toward the margin as an independent vein. Comparison with these two families shows that in the remaining Adephaga the apex of Cu has disappeared by atrophy, while the double trachea suggests that in the Polyphaga it has fused with M_4 .

First anal.—This is simple. With the atrophy of its base the cross-vein cu-a remains to connect it with the stem of cubitus (Hylecetus, Fig. 40). In some forms, as in the Lampyridæ (Fig. 32) it is not clear whether it is the base of the main vein or the cross-vein, which has disappeared.

Second anal.—The second anal trachea divides, at the maximum, into three branches. The first corresponding vein has been universally considered a branch of the vein here designated 1st A, but if that is the case the extraordinary course of its trachea, which actually has to turn basad in some Buprestidæ, to enter its cavity, and which may run for some distance in a common vein-cavity with the first anal trachea without fusing with it, remains entirely unexplained. This first branch is doubtless the one that has disappeared in the Tenebrionidæ and Adephaga (where there is no corresponding trachea); but in the higher Phytophaga it seems rather to be 1st A that has vanished, as there is no trace of a first anal trachea arising from Cu. The second branch of 2d A has nothing extraordinary, and receives the unbranched second anal trachea in the Tenebrionidæ (in some specimens only of which the third branch also receives a tracheal twig). The third branch has apparently evolved in two distinct ways. In a few forms it is entirely independent (as in Attagenus, Fig. 35, and many Buprestidæ, Fig. 34). The next, and perhaps most primitive condition, is for it to be connected by a cross-vein to the upper fork of 3d A, as plainly shown in *Cebrio* (Fig. 30). It is my belief that the same condition holds in the other Elateridæ (s. l.) and Lampyridæ, where there are three anal twigs below the second anal furrow, and the vein bounding the wedge-cell is transverse and tends to disappear by atrophy (Alaus, Pyrophorus, Calopteron). In most forms, however, the apex of this branch has

obviously fused with the first branch of 3dA, forming a pointed wedge-cell, and leaving only two terminal branches below the second anal furrow (compare Figs. 32 and 37).

On the basal side of the wedge-cell there is a short oblique vein running from the stem of 2d A to the upper branch of 3d A. Whether this is a fourth branch of 2d A, which has permanently joined 3d A₁, or a cross vein, is not clear. Occasionally it contains a trachea arising from 2d A, but tracheæ in other crossveins are not entirely unknown. In the pupa of *Tenebrio* and *Dytiscus* it is more definitely transverse than in the imago, a significant point.

Third anal.—The third anal vein forks once near the base of the wing as a rule. Sometimes both branches have a trachea, sometimes only the lower. The upper is connected to 2d A by two transverse veins, enclosing the wedge-cell between them. In a few forms the third anal is simple, presumably by the atrophy of its upper branch, which is broken, for instance, in the Lamellicorns (Fig. 62).

Fourth anal.—The anterior branch of the fourth anal vein is present in all save markedly reduced species, and contains a trachea in all species with fairly complete tracheation. A second branch is present in most Adephaga, running along the inner margin of the wing, and in a few a third, running back and stiffening the alula. This is the superficial interpretation; it is not impossible that a detailed comparison with the Neuropteroids will result in a different interpretation. In particular the vein here considered 3d A₂, may possibly belong in fact to 4th A.

CROSS-VEINS.

It is evident that the Coleoptera are descended from a form with a considerable number of cross-veins, which were tending at least to take definite positions. Assuming that they were not wholly definite, the survival of certain ones was doubtless determined by the folding, which necessitated a more complete cross-bracing than in the Trichoptera and Lepidoptera, for instance. The humeral has already been taken up. Discussion of other cross-veins in the costal region would be useless, as the longitudinal veins are almost completely fused. Comparison with the Neuroptera would prepare one for a large number of such veins, but the few forms in which C and Sc are separate (e. g., *Cupes*, Fig. 12) show no sign of them.

Between R₁ and R_s there is plain evidence of several cross-veins. For the region basad of the pivot-fold, the Hydrophilidæ, and especially the primitive Elaters, give the best evidence. They plainly show two cross-veins, one variable in position, but well before the fold of the wing, the other stiffening the edge of the first fold, being the outer part of the vein marked R_{s+r} in Fig. 30. The latter is obscurely indicated in several Adephaga, but there is no trace, apparently, of the first, the radial fork coming just before the hinge.

Beyond the hinge the Hydrophilidæ show only faint traces of veins, and most Polyphaga none at all; but the Adephaga have two well-developed cross-veins, which may be called 3d r and 4th r. The

vaguely defined vein which stiffens the fold half way between the last and the apex in the Gyrinidæ, for instance, would then be 5th r.

There would be possible a second explanation of these veins; namely, that the pivot fold of the Adepfaga corresponds not to that of the Hydrophilidæ and Tenebrionidæ, etc., but to that of the Coccinellidæ and Malachiidæ. This would reduce the number of radial cross-veins postulated, as it would make the two main cross-veins of the Adepfaga homologous with the two of the Polyphaga, but it would involve a reversal in direction of the two principal transverse folds. It would also leave the faint cells of Hydrous unexplained. This interpretation seems to me less probable, but must be taken into account, considering the variable character of the folding in all parts of the wing. There is much room for some one with care and patience to make a study of the wing folding, which shows much more variety of type than Woodworth's account would imply. The forms intermediate between the Adepfaga and Polyphaga (Staphyloidea in the broad sense; Figs. 24 to 28) are all highly modified, and many of them minute, with reduced venation; so that very careful analysis will be necessary to interpret them.

Between radius and media (as interpreted by the tracheæ) the Adepfaga have single fully formed cross-vein, marked r-m. In some species of Cupes this has migrated far toward the base of the wing, (Fig. 4), but in other species (Fig. 12), and in Omma, it is normal. In a few Elaters (Fig. 30), it is plainly shown, as a distinct, though faint, vein connecting the base of R_s with M, but as a rule in the Polyphaga it is lost, or incorporated indistinguishably in the radial recurrent. (Compare Hydrocharis, Fig. 22, with Hydrous, Fig. 20).

The obvious cross-vein of the Polyphaga appears to be a second, the surviving element of a complex net-veined area, apparently, which is faintly visible in some Cerambycidæ and Chrysomelidæ, but has been mostly obliterated to form the large and complexly folded central cell. Aside from the Phytophaga a few other forms show aberrant veins or thickenings that may be remnants of this system, notably the Cupedidæ (Figs. 4, 12) and Ostomidæ (Fig. 49). How much is original and how much secondary in the complicated conditions of the Malachiidæ (Fig. 58) and Coccinellidæ (Fig. 56) may sometime appear from more detailed study, or the discovery of transitional forms.

A third radiomedial cross-vein is indicated at the outer boundary of the central cell, connecting the stem or stub of R_{4+5} with M_1 . It must be through the survival of this cross-vein that R_{2+3} in the Lamellicornis gets its connection with the medial stem.

There are two medio-cubital cross-veins, enclosing the so-called *Oblong* cell (O) of the Adepfaga and Cupedidæ. The more basal of these may receive a trachea from media, but I am inclined to consider this not significant, as the assumption that it is really the stem of M_{3+4} will not work out into any logical interpretation of the marginal veins. In the more specialized Adepfaga (Fig. 13) and the Hydrophilidæ there is only one cross-vein. The usual explanation is that one or the other has atrophied. It seems more simple to assume the

two have fused, especially as in several Carabidæ there is a partial fusion. The families in which there is a single cross-vein are the Cicindelidæ (save the genus *Pogonostoma*, as figured by Horn, Gen. Ins., 82, pl. 5, f. 52), Rhyssodidæ and Hydrophilidæ, with a few stray genera of other families. In the remaining Polyphaga the cross-veins are obliterated by the fusion of M_4 with Cu.

The cross-vein cu-1st a is mentioned under the discussion of that vein. In Cupes alone there is a second cubito-anal cross-vein in the outer part of the wing.

A very important cross-vein is the one from the base of 1st A or from the fused root of Cu_4 +1st A to the base of 2d A. It is doubtless homologous to the anal cross-vein of the Trichoptera and lower Lepidoptera. In all forms but the Cupedidæ the extreme base of 1st A is transverse and appears (with the disappearance of a sector of 1st A) as a part of it. I will refer to this combined vein as the anal arculus (a. arc.) as its relation to 1st A is exactly that of the arculus to media in the Odonata and some other orders. This vein appears in all the Adepaga and Staphylinoidæ, excluding the Histeridæ, but nowhere else. Another cross-vein 1st-2d a appears in the outer part of the wing in Cupes oculatus (Fig. 12), but in most other Coleoptera it is obliterated by the anastomosis of the anterior branch of 2d A with 1st A.

Two cross-veins may be assumed between 2d A and 3d A, enclosing the wedge-cell (W) between them, but as noted in the discussion of 2d A, it is not quite certain that the inner is a cross-vein, and the outer is preserved only in the Elateridæ, Lampyridæ, and a few related forms.

There is in the Cupedidæ and Adepaga a transverse vein at the extreme base between 3d A and 4th A, but its significance is uncertain.

FOLDING.

I figure folding diagrams of a few typical Coleoptera (Figs. 7, 16, 21, 25, 27, 61). In these the portions of the wing reversed (turned under or over) in the folded wing are shown dark, those which remain right side up are white. Convex folds are indicated by a broken or serrate line, concave by an even line. Regions of irregular crumpling, and regions not completely folded under, are striated.

It can be seen that the folding is highly complex, and may differ in details in closely related forms, though of the same fundamental plan (compare especially *Harpalus*, Fig. 16, with *Dytiscus*, Fig. 7). The Dytiscid and Hydrophilid foldings are homologized by d'Orchymont differently than by me, with the result that he considers the vein I call media in the Adepaga to be rather the radial recurrent. I have given first weight to the fact it always contains the medial trachea, and have assumed that the area at the hinge that folds under has become more extensive in the Adepaga, and has crossed the medial vein. It should be also noted that the area homologous with the reversed portion in the cell of the Adepaga is not the large reversed portion of the Polyphaga, but the relatively inconspicuous crumpled strip

above cubitus, as shown by the fact that it alone constantly reaches the base of the wing. *Hydrocharis* (Fig. 22) and other forms with a short radial recurrent, show the condition better than *Hydrous* (Fig. 21).

DISCUSSION OF CERTAIN FORMS.

It is not the province of one not a Coleopterist to go into the detailed discussion of the relationships of the Coleopterous groups, but some points come out so clearly that they should be emphasized. First it is strikingly clear that Gahan's system comes far nearer to agreeing with the evidence of the wings than any other known to me.

Adephaga.—(Figs. 2, 3, 5, 7, 10, 11, 13–19): If venation means anything at all this is a homogenous group, and includes the *Rhysodidæ* as a hardly aberrant member. Whether the *Cupedidæ* should also be included is a discussed question. They certainly have one point of divergence from all the typical *Adephaga* in venation, namely, the preservation of the first branch of 2d A as an apparent branch of 1st A. The *Haliplidæ* alone of the forms examined have preserved the tip of Cu; as have the *Pelobiidæ* as figured by d'Orchymont. The sub-families of *Carabidæ* are not obviously indicated by the venation, even *Pseudomorpha* being hardly aberrant. Fragments of 2d r appear in a few forms (*Harpalus*, Fig. 15). R_{4+5} often appears as a strong stub (Fig. 13) but never bears terminal branches. *Amphizoa* does not differ obviously from *Dytiscus*, both having a long straight 1st A, with a thickening below it. The *Gyrinidæ* differ mainly in having a thickening above the outer part of the stem of M, of uncertain significance. It might be interpreted as a trace of M_{1+2} , but this would not lead to any logical working out of the distal part of the wing.

Cupedidæ.—(Figs. 4, 12). The characters of this family have been abundantly discussed. The difference between the superficially almost identical species *C. capitatus* and *C. oculatus* is curious. Note especially 1st r-m, 2d A_1 , the wedge-cell, and the position of the anal cross-veins.

Staphylinoidea.—*Silpha* (Figs. 24, 25) and *Necrophorus* are closely related, in fact almost identical in venation as well as wing-folding, and show a marked resemblance to the *Staphylinidæ* (Fig. 28). Note the preservation of the anal arculus, the principal fold of the wing lying before the thickened stigma, and the simplified anal region without any visible connection between 2d A and 3d A. There is practically nothing to connect this group of families with either the *Adephaga* or higher forms, and they might well be a survival of some earlier type. The alula of the elytron is preserved, as in the *Adephaga* and *Hydrophilidæ*. The folding is unique, but perhaps a little more easily interpreted as *Adephagous*.

Brathinus, an interesting intermediate form in body characters, is too reduced to have a significant venation.

Necrophilus (Figs. 26, 27) is far more widely separated from *Silpha* than it from the *Staphylinidæ*. The folding is unique (Fig. 27), the wing folding over just beyond the stigma. The genus, while perhaps

Silphid, is obviously out of place between Silpha and Necrophorus. I believe the small Silphidæ will go with it; Prionochæta at least shows essentially the same wing.

Palpicornia.—(Figs. 20-23). This group is interesting as alone showing a complex apical venation, as well as being the only one of the Polyphaga to preserve traces of the radial cells beyond the fold. The folding at the costal margin is as in the Adephaga while the remainder of the wing is almost typically Polyphagan. The radial recurrent obviously belongs more to the first r-m than to the base of Rs, in several genera almost connecting with the stem of M. One anal (2d A₁) is always lost. The family is primitive in preserving M₄ and Cu as separate veins, like the lower Adephaga and perhaps the Staphylinioidea, but unlike all the higher forms.

The smaller genera (such as Sphæridium, Fig. 23) show a striking resemblance to the Lamellicorns, that may possibly be significant, as the latter show distinct traces of distal veining.

Buprestidæ.—(Figs. 6a, 34). A student here is working on this family, which as Gahan notes shows no close resemblance to the Elaters. It is evidently a survival, and is one of the very few that has three free branches to 2d A. The lack of folding of the wing is not characteristic of the family as a whole, since Brachys folds normally.

Elateroidea.—(Figs. 30-33). The Elateridæ (Fig. 31) and Lampyridæ (Fig. 32) form a very well defined group in venation, to which all the small families of Sternoxia but the Rhipiceridæ will attach themselves. Cebrio (Fig. 30) is most primitive, and basic for interpreting the anal region. A general characteristic is the transverse outer end of the wedge cell (which fails in several genera by the loss of the cross-vein, and in Tharops alone by its obliquity). Another is the position of 1st r in all but a few aberrant groups markedly basad of the radiomedial. The folding is also uniform, being a double chevron-fold in the apex, rather like that of the Heteromera and lower Buprestidæ, but utterly unlike the Malachiidæ. The Lampyridæ are exactly like the most specialized Elaters, differing from the typical ones only by the loss of the cross vein cu-a. If the venation means anything they are degenerate rather than primitive.

Malachiidæ (Melyridæ).—(Figs. 57, 58). These so far as the wings show have nothing whatever to do with the Lampyridæ, and may be a survival of a primitive type, especially if the transverse vein from the cell to the inner margin is really an independent Cu. The folding is very complicated and I have not worked it out fully. The nearest thing to it seems to be in the Coccinellidæ (Fig. 56). There are two pivot-folds at the costa, the more posterior of which corresponds in its manner of folding with that of the Adephaga and Hydrophilidæ, the more anterior with that of the Bostrychidæ and Byrrhidæ. The anal region is degenerate and gives no help. A large South American species shows no more veins than Malachus.

Dascyloidea.—(Figs. 37, 38). The Dascyloidæ and Rhipiceridæ are almost identical in venation, and distinguished mainly by the lack of the special characters of the other groups, in this resembling the lower

members of the Clavicornia, and the Macroductylia. At present several members of this group are considered Buprestidæ and one or two primitive Elateroids are standing as Dascyllidæ. The Helodidæ are not even remotely related, but vaguely suggest the Dryopidæ and the Niti-dulidæ.

Macroductylia.—(Figs. 41, 42). It is an utter mystery to me how Kolbe, with any consideration of the venation, could separate the Parnidæ in three distinct superfamilies. There are differences, but they are mainly of the character of degree of development, and could be matched in almost any family of Coleoptera containing small species. He seems to have particularly emphasized the development of the medial recurrent. In venation the series has no particular characters, unless perhaps the tendency for R_3 to be stronger than M_1 . Psephenus has preserved a radial cross-vein, while the European Dryops viennensis (Fig. 41) has preserved the usual five anals in the main group, which are reduced in the others. The folding is based on the Hydrophilid type, but this may not be significant, as this was presumably the original type for the Polyphaga generally; the preservation of $2d A_1$ forbids derivation directly from the Hydrophilidæ.

Lymexylonidæ (Fig. 40).—I have only been able to study two forms. Hylecœtus tenebroides has nothing aberrant about it, and could perfectly well belong to the Heteromera, which themselves are not widely unlike many other Serricornes. Atractocerus is so modified as hardly to be significant, and is strangely suggestive of the Meloidæ, but could equally be derived from Hylecœtus.

Cleridæ.—(Fig. 48). This family, which with the Malachiidæ makes up the Trichodermata, shows none of the primitive characters of the Malachiidæ. On the other hand it is not strongly distinguished in venation from the Ostomidæ.

Dermestidæ.—(Figs. 35, 36). The Dermestids show at least three radically different types of venation. Attagenus (Fig. 35) is primitive in having the wedge-cell open by the lack of fusion of $2d A_3$ and $3d A_1$, as well as in the presence of an ocellus. It resembles nothing else whatever. Dermestes (Fig. 36), represents the ordinary Dermestid type, and while well characterized, it would not be out of place in the Dascylloids so far as venation is concerned. The $2d$ anal furrow seems however, to have three veins below and two above it, which would suggest a more primitive position for it also. Anthrenus is reduced, but offhand would suggest another family type, nearer the normal clavicorns.

Byrrhidæ (Figs. 51, 52).—These do not suggest the Dermestidæ at all in venation, nor anything else I have studied except possibly Mycetophagus. There are two pivot-folds, as in the Malachiidæ, but otherwise no very close likeness. The Mycetophagidæ (Fig. 53) are more primitive in preserving the wedge-cell, the Byrrhidæ in having cross-vein cu-a. Both show traces of complexity in the vein r-m, but this may be a secondary effect of the folding.

Ostomidæ (Trogositidæ) (Figs. 49, 50).—The most distinctive character of this family seems to be a tendency to chitinize the area of the wing crossed by r-m, in the form of an arrowhead-shaped mark,

exactly as in the Cleridæ, and to a rather strong preservation of the tip of M_1 . A chitinization beyond the pivot-fold alone gives a slight special likeness to the Hydrophilidæ, with which they agree in type of folding.

Heteromera (Figs. 6, 43-46).—There is nothing about the venation of the Heteromera to separate them in two groups corresponding to those in Leng's Catalogue, and on the whole not much that is distinctive. The folding, as in the Hydrophilidæ, Buprestidæ, Elateroidea, Dascyloidea, Dermestidæ, Macroductylia, etc., is of what may be called the normal type, dominated by a double pivot fold in the same position as in the Adephaga. The venation of the same region is rather simple, and possibly nearest to the Buprestidæ which fold their wings, and the Ostomidæ. In the anal region $2d A_1$ is invariably lost, but the type is that normal in families mentioned, in other points. The *Erotylidæ* have the same venation, and should be re-examined as to homogeneity as a family, as some of them have heteromerous tarsi.

Meloidæ.—The Meloidæ (Fig. 47) at first sight are markedly divergent from the remainder of the Heteromera; but the points of divergence seem merely to be the result of reduction. The radial cell is lost, and the outer ends of the radial and medial recurrents have become nearly transverse, and continuous with the radiomedial cross-vein, giving a characteristic appearance to the outer part of the wing. In the anal region there are three simple veins, with a chevron-shaped structure between the second and third, toward the base. At first sight this arrangement seems unique, but is easily derivable from the normal heteromerous type by the loss of the lower side of the wedge-cell and vein $2d A_{3+3d} A_1$. The Trictenotomidæ of Africa seem to be intermediate.

The *Rhipiphoridæ* have so completely lost their veining that they might be interpreted in any way. The few traces of veins left are not specially suggestive of the Meloidæ, but the other characters and habits place the family in this neighborhood. The *Stylopidæ* are also extremely reduced; but the venation, so far as preserved, seems to agree with that of the Meloidæ.

Nitidulidæ (Figs. 54, 55).—*Phenolia grossa* is a reduced form, but with an extraordinarily complex type of folding, which I have not tried to work out in detail. The recurrents form a deep loop, exactly as in the Histeridæ, but the character is as likely as not to be due to convergence, as the forms have no other special likeness.

Histeridæ (Fig. 29).—Ganglbaur by some extraordinary slip put this family in the Staphyliniformia on venational characters, stating that the medial recurrent is absent. In fact M_r is an exceptionally strong and heavy vein, as well as R_r , and both appear to take part in the folding of the wing, which resembles the Staphylinidæ in no way. Save for the preservation of R_5 as a vein in the outer part of the wing, the form would be easily derivable from the other clavicorns, by an increase of the folded portion. In any case, as there is no trace of the anal arculus, and the recurrents are fully developed, the relationships

of the form are to be sought in the latter families and not in the Staphyliniformia.

Coccinellidæ (Fig. 56), *Endomychidæ*.—These two families agree in the curious anal system formed of two loops, and the curious manner of folding, with two hinge-folds working together. The venation is adjusted to this folding, and reduced, even in species as large as *Epilachna*, so that except as it emphasizes the isolation of the family the venation is of little use. What likeness there is, is to the *Malachiidæ*.

Bostrychoidea (Figs. 59–61).—The *Bostrychidæ* are characteristic, and the *Ptinidæ* resemble them closely. The folding is very simple (Apaté, Fig. 61) and derived from a type with anterior pivot-fold, such as the *Melachiidæ*. In venation the principal character is the origin of M_1 directly from the cross-vein, whereas it is free in almost all the other *Polyphaga*. *Dinapate* is not aberrant in the least.

Lamellicornis (Fig. 62).—All the *Lamellicornis* have a single type of venation. There is a strong tendency for the central cell to be obvious, and to keep its rounded form, and R_3 frequently switches its attachment from the upper to the lower side of it, as in the figure. The anal region is characterized especially by the reduction of the upper fork of $3d A$ to a short stub running across toward $2d A$, the complete disappearance of the wedge-cell, and the detachment of $1st A$ and the two upper branches of $2d A$, which show as fine chitinous streaks or disappear entirely. I have seen no form in which all three were distinct; in some $1st A$ is visible close to the junction of M_4 with Cu (Kühne, Fig. 21), in others it is $2d A_1$ that is preserved; $2d A_2$ is usually present. The radial cross-vein appears always to be absent, but the apical system of veins are more distinct than in any other family save the *Hydrophilidæ*, R_{4+5} often showing as a distinct stub, connected with R_{2+3} , and Mr showing a decided angle at the point where M_1 is presumably given off.

In general the *Trogidæ* and *Lucanidæ* have a larger cell below the base of $2d A$, but the families are not well separated in venation.

Phytophaga (Figs. 63–68).—This group tends strongly to simplification of the anal region, but the lower forms are quite typical. There is, with a few exceptions, a spur on the outer side of $r-m$, and rarely one on the inner side also, or even more complex structures involving the first radiomedial as well. The central cell is apt to be well-outlined, and M_1 usually is strongly developed and attaches to it. Aberrant forms, however, like *Distenia undata*, figured, violate all the definitions of the group, and make it undefinable on venation. In *Prionus* the anal region is almost like that of *Hydrous*. On the other hand the typical venation, with a spur on the second radiomedial cross-vein, is universal in the *Chrysomelidæ* and *Mylabridæ* (*Bruchidæ*) and is carried over into the *Anthribidæ* of the *Rhynchophora*, whose position in the group cannot be challenged. The higher *Rhynchophora*, of course, are highly modified in connection with their peculiar wing folding, though even they show some slight trace at times of the characteristic spurred cross-vein.

The folding is of the *Hydrophilid* type.

SUMMARY.

The venation of the Coleoptera is based on the same fundamental plan as that of the Neuroptera and other Holometabola, but with a rather large number of cross-veins. Costa is typical, not always marginal; subcosta normal, concave, usually fusing with radius; radius with R_1 obsolescent, fusing with Sc, R_s sharply divergent from R_1 at origin, and usually obsolescent at root, then broken by the principal fold of the wing, R_2 and 3 represented by parallel more or less rudimentary veins toward the costa, R_{4+5} bending down sharply on the outer side of a *central cell* where all the folds of the wing tend to converge, then turning out, and when complete ending in one branch near apex and one far below, near M_1 . (Hydrophilidæ, Histeridæ), usually reduced to a short stub (Adephaga, Scarabæoidea) or lost. Media oblique from R to Cu near root, then obsolete a distance, then showing as a spur attached at its apex to Cu, in the outer part of the wing with two divergent branches, representing M_1 and M_4 ; Cu simple, strong to fold, then usually lost beyond or fused with M_4 ; anals complexly anastomosing, typically with 6 or 7 terminations, of which only one belongs to 1st A.

The Haliplidæ are generalized among the Adephaga, the Amphizoidæ very close to the Dytiscidæ.

The Hydrophilidæ contrast with all the other Polyphaga in the preservation of both M_1 and Cu, and often in a more or less complete apical venation. Sphæridium suggests the Lamellicorns.

The Silphidæ are very near the Staphylinidæ in venation; the Necrophilus group less close. They form an isolated group apparently not nearer the Polyphaga than Adephaga.

The Histeridæ have nothing to do with the Staphyliniformia, but are Clavicorn or isolated.

The Elateridæ and Lampyridæ are closely related, and the venation suggests that the Lampyridæ are degenerate from an early elater type, not primitive.

The Malachiidæ, Coccinellidæ and some other families seem to make a separate group, which certainly has nothing to do with the Lampyridæ or Cleridæ.

The Rhipiceridæ are Dascylloid, not Elateroid, as noted by Gahan.

The Cleridæ are possibly related to the Ostomidæ.

The Lymexylonidæ are not especially generalized, and suggest the point of origin of the Heteromera.

The Heteromera show no sign of double origin where now divided; the Meloidæ on the other hand, contrast strongly with the families associated with them, apparently resembling the Rhipiphoridæ and Stylopidæ.

The Clavicornia are a heterogeneous group, on which light will certainly be thrown by the venation and folding.

EXPLANATION OF PLATES.

ABBREVIATIONS USED.

C—Costa.	4thA ₂ —Presumed second branch of fourth anal.
Sc—Subcosta.	hum—humeral cross-vein.
Sc ₁ , Sc ₂ —its branches.	arc—arculus.
R—Radius.	a. arc—anal arculus (cross-vein 1st-2d and base of 1st A).
R ₁ , R ₂ , R ₃ , R ₄ , R ₅ —its branches.	r—radial cross-veins.
Rs—Stem of radial sector.	r-m—radiomedial cross-veins.
M—Media.	m-cu—mediocubital cross-veins.
M ₁ , M ₂ , M ₃ , M ₄ —its branches.	cu-a—cubitoanal cross-veins.
1st A—First anal vein.	1st-2d a, 2d-3d a—interanal cross-veins.
2d A—Second anal vein.	O—Oblong cell (2d M).
2dA ₁ , 2dA ₂ , 2dA ₃ —its branches.	W—Wedge-cell (2d 2d A).
3dA—Third anal vein.	st—Pterostigma.
3dA ₁ , 3dA ₂ —its branches.	
4thA ₁ —Fourth anal vein.	

PLATE XXIX.

- Fig. 1. Hypothetical plan of wing venation of Coleoptera, based mainly on Cupes (base and cell), Cebrio (anal region) and Hydrophilus (apex). The conventional symbols for the veins and cells are used, namely:
- Fig. 2. Tracheation of wing of imago of Calosoma species. The tracheæ are shown as solid lines, the veins stippled.
- Fig. 3. Tracheation of imago of Dytiscus verticalis.
- Fig. 4. Venation of Cupes capitata.

PLATE XXX.

- Fig. 5. Tracheation of young pupa of Dytiscus, from a preserved specimen. The tracheæ are shown so far as made out, by solid lines, the vein-cavities stippled. The specimen is imperfect and a fresh wing would probably show more tracheæ and veins.
- Fig. 6. Tracheation of young pupa of Tenebrio molitor (about one day after pupation). The tracheæ are all as shown in one mount, the veins restored by comparison with the late pupa and imago.
- Fig. 6a. Tracheation of young pupa of Agrilus ruficollis. Slide by Henry Good.
- Fig. 7. Diagram of wing-folding of Cybister. The portions of the wing reversed in folding are shown black. Concave folds are indicated by even lines, convex ones by toothed lines. Regions of the wing, which are half folded over, or crumpled, are hatched.
- Figs. 8, 9. Folded wing of Apathe capucina (Polyphaga, Bostrychidæ); the veins cross-hatched and concealed portions dotted in. Dorsal and ventral views.
- Figs. 10, 11. Folded wing of Colymbetes sculptilis (Adephaga, Dytiscidæ); like Figures 8 and 9. Dorsal and ventral views.

PLATE XXXI.

- Fig. 12. Cupes oculata (Cupedidæ). Slide by courtesy of C. T. Brues.
- Fig. 13. Tetracha virginica (Cicindelidæ).
- Fig. 14. Galerita janus (Carabidæ).
- Fig. 15. Harpalus caliginosus (Carabidæ).
- Fig. 16. Same; folding plan (compare Figure 7).
- Fig. 17. Pheropsophus æquinoctialis (Carabidæ; South America).
- Fig. 18. Trogus glaucus (Dytiscidæ; South America).
- Fig. 19. Cnemidotus edentulus (Halipilidæ).
- Fig. 20. Hydrous triangularis (Hydrophilidæ).
- Fig. 21. Same, folding plan (compare Figure 7).
- Fig. 22. Hydrocharis obtusatus (Hydrophilidæ).
- Fig. 23. Sphæridium scarabæoides (Hydrophilidæ).

PLATE XXXII.

- Fig. 24. *Silpha* species (Silphidæ).
 Fig. 25. Same. Folding plan (see Figure 7).
 Fig. 26. *Necrophilus hydrophiloides* (Silphidæ?).
 Fig. 27. Same. Folding plan (see Figure 7).
 Fig. 28. *Staphylinus maculosus* (Staphylinidæ).
 Fig. 29. *Hister inæqualis* (Histeridæ; Europe).
 Fig. 30. *Cebrio bicolor* (Cebriionidæ).
 Fig. 31. *Elater discoideus* (Elateridæ).
 Fig. 32. *Photuris pennsylvanicus* (Lampyridæ).
 Fig. 33. *Pactopus hornii* (Throscidæ).
 Fig. 34. *Dicerca lurida* (Buprestidæ). Slide by Henry Good.
 Fig. 35. *Attagenus pellio* (Dermestidæ).

PLATE XXXIII.

- Fig. 36. *Dermestes marmoratus* (Dermestidæ).
 Fig. 37. *Sandalus porosus* (Rhipiceridæ).
 Fig. 38. *Dasyllis plumbeus* (Dasyllidæ).
 Fig. 39. *Cucujus clavipes* (Cucujidæ).
 Fig. 40. *Hylecoetes tenebroides* (Lymexylidæ; Europe).
 Fig. 41. *Dryops viennensis* (Dryopidæ; Europe). Our species have lost 2d A₁.
 Fig. 42. *Heterocerus pallidus* (Heteroceridæ).
 Fig. 43. *Tenebrio molitor* (Tenebrionidæ).
 Fig. 44. *Penthe pimelia* (Melandryidæ).
 Fig. 45. *Mycterus scaber* (Melandryidæ).
 Fig. 46. An undetermined species representing the Cistelidæ.
 Fig. 47. *Pomphopoea sayi* (Meloidæ).

PLATE XXXIV.

- Fig. 48. *Trichodes apivorus* (Cleridæ).
 Fig. 49. *Trogosita virescens* (Ostomidæ).
 Fig. 50. *Tenebroides* sp. (Ostomidæ).
 Fig. 51. *Byrrhus* sp. (Byrrhidæ).
 Fig. 52. *Nosodendron unicolor* (Byrrhidæ).
 Fig. 53. *Mycetophagus* species (Mycetophagidæ).
 Fig. 54. *Glischrochilus fasciatus* (Nitidulidæ).
 Fig. 55. *Phenolia grossa* (Nitidulidæ).
 Fig. 56. *Coccinella transversa* (Coccinellidæ).
 Fig. 57. *Malachius aeneus* (Melyridæ; Europe).
 Fig. 58. *Collops bipunctata* (Melyridæ).
 Fig. 59. *Dinapate wrighti* ♀ (Bostrychidæ). Slide by courtesy of Henry Dietrich.

PLATE XXXV.

- Fig. 60. *Apate capucina* (Bostrychidæ; Europe).
 Fig. 61. Same. Folding diagram; compare Figures 7, 8 and 9.
 Fig. 62. *Lucanus dama* (Lucanidæ).
 Fig. 63. *Asemum nigrivenum* (Cerambycidæ).
 Fig. 64. *Distenia undata* (Cerambycidæ).
 Fig. 65. *Leptura canadensis* (Cerambycidæ).
 Fig. 66. *Caryoborus arthriticus* (Mylabridæ-Bruchidæ).
 Fig. 67. *Donacia aequalis* (Chrycomelidæ).
 Fig. 68. *Entomoscelis adonidis* (Chrysomelidæ).
 Fig. 69. *Neuronia* species (Trichoptera). Hind wing for comparison with the hypothetical type of the Coleoptera.
 Fig. 70. *Chorista australis* (Panorpata; Choristidæ; Australia). After Esben-Petersen. Hind wing.
 Fig. 71. *Chauliodes pectinicornis*. (Neuroptera; Sialidæ). Hind wing.